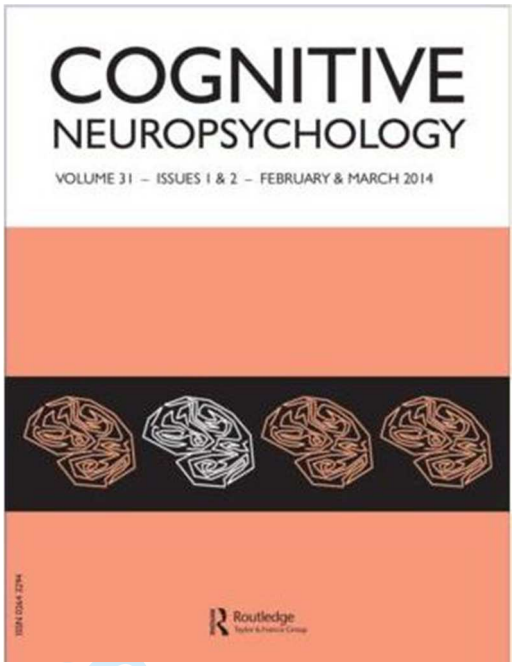


# The vestibular body: vestibular contributions to bodily representations

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# The vestibular body:

# vestibular contributions to bodily representations

**Abstract**

Uniquely among the sensory modalities, vestibular inputs do not project to any primary unimodal cortex. Rather vestibular signals are integrated with signals from other sensory modalities, such as vision, touch and proprioception. This convergence could reflect an important mechanism for maintaining the perception of the body. Neuropsychological, electrophysiological and psychophysical studies show support for this hypothesis. Here we review the current literature in order to develop a framework for understanding how the vestibular system contributes to body representation. According to recent models, we distinguish between three processes for body representation, and we look at whether vestibular signals might influence each process. These are (i) *somatosensation*, the primary sensory processing of somatic stimuli, (ii) *somatoperception*, the processes of constructing percepts and experiences of somatic objects and events and (iii) *somatorepresentation*, the knowledge about the body as a physical object in the world. Vestibular signals appear to contribute to all three levels in this model of body processing. Thus, the traditional view of the vestibular system as a low-level, dedicated orienting module tends to underestimate the pervasive role of vestibular input in bodily self-awareness.

**Abbreviations:**

OP: Parietal Operculum

PIVC: Parieto-Insular-Vestibular Cortex

SEPs: Somatosensory Evoked Potentials

LEPs: Laser Evoked Potentials

BIID: Body Identity Integrity Disorder

**Keywords:**

Vestibular system; multisensory integration; body representation.

## Introduction

Our body is the object we know best. Not only do we have more information on our body compared to any other objects, but we also have a privileged access to our own bodily sensations that we cannot have for any other bodies or objects (Eilan et al., 1998). It might not be surprising therefore that few issues in cognitive neuropsychology and experimental psychology have encountered such interest as how the brain represents our body. Current research has accumulated a large body of evidence showing that coherent body representations are generated by the successful integration of multimodal sensory signals (Blanke and Metzinger, 2009; Blanke, 2012). Strong emphasis has been traditionally put on the two classical signals which tell us about the body: vision and touch. Only recently have studies highlighted the essential role played by our sixth sense, the *vestibular system*, in the perception and representation of the body.

The vestibular system provides continuous information to the brain to update body position and to maintain orientation in the surrounding space (Berthoz, 1996). The semicircular canals detect rotational movements of the head in three-dimensional space (i.e., pitch, yaw and roll) and the otolith organs (utricle and saccule) code translational acceleration, including the orientation of the head relative to the gravitational vertical. These signals are highly relevant to several interactions between the organism and the environment. In particular, dynamic vestibular inputs from the canals are associated with low-level visuo-vestibular interactions to control gaze and eye fixation, while static gravitational inputs from the otolith organs contribute to path integration and navigation. Accordingly, vestibular peripheral dysfunction leads to disintegration in the normal relation between personal and extra-personal space (Blanke et al., 2004), confirming a vestibular contribution to the brain's *Global Positioning System.*

Vestibular signals are *somatic* in two distinct senses. First, they continuously detect movement and acceleration of the head and the body. Second, vestibular signals may also provide a more general experience of our body. Vestibular receptors are directly sensitive to gravitational accelerations, and they have been shown to play a crucial role in sensing the

vertical direction of gravity (Böhmer and Mast, 1999; Bronstein, 1999; Mittelstaedt, 1991; Mittelstaedt, 1992; Mittelstaedt, 1999; Snyder, 1999; Barnett-Cowan et al., 2015). The perception of verticality is based on the integration of somatic information generated by vestibular receptors in the inner ear with signals from the muscles, joints, skin, and viscera (Lackner, 1988; Lackner and DiZio, 2005; Mittelstaedt, 1992; see Lacquaniti et al. 2015 for a review). The well-known *Aubert effect* is a clear example of such a vestibular-somatic relation (Anastasopoulos et al., 1999; Yardley, 1990): when a person is roll-tilted, and deprived of relevant visual cues about their orientation, the subjective perception of gravitational vertical is biased towards the body axis. That is, the online perception of verticality seems to include a strong prior that the body is upright, as well as sensory afferent information. A stronger bias towards the body midline could be taken as evidence for a weaker sensory verticality signal input, so the contributions of priors and sensory evidence to verticality perception can be measured. Several studies have shown that the online sensory evidence in the Aubert situation is not only vestibular, but also somatosensory. For instance, case reports showed that patients with entire sensory loss and patients suffering from hemisensory loss lying on their impaired side did not exhibit the normal Aubert effect when tilted in the way that normally induces such effect (Anastasopoulos et al., 1999; Yardley, 1990). This suggests that vestibular inputs are strongly combined with other somatic signals even for the processing of percepts, such as verticality, that are classically considered purely vestibular.

Uniquely among the sensory modalities, vestibular inputs do not project to any unimodal cortex. Multimodal convergence has been described in almost all vestibular relays, including the vestibular nuclei, the thalamus and several areas in the cerebral cortex (zu Eulenburg et al., 2012; Lopez et al., 2012a). Electrophysiological studies have identified a widespread vestibular network whose core area is the Parieto-Insular-Vestibular Cortex (PIVC). This area lies in the posterior parietal operculum extending into the posterior insular lobe (Guldin and Grüsser, 1998). The human homologue of the primate PIVC is a distributed set of

regions including the posterior and anterior insula, temporo-parietal junction, superior temporal gyrus, inferior parietal lobule, and somatosensory cortices (see Lopez et al., 2012a for a review). This network can be divided in three main functional components (Balaban et al., 2011). First, a *sensorimotor component* which includes pathways for the sensory integration and perceptual responses of vestibular, visual, proprioceptive and somatosensory information and for both somatic and visceral motor response mechanisms (Balaban and Yates, 2004). Second, a *cognitive component* which includes pathways for regulation of affect, decision making, attention and higher cognitive behaviours. Third, an *interoceptive component* which includes pathways for the integration of information regarding ongoing sensory processes relative to the current physiological condition of the body (Balaban et al., 2011).

Several neuropsychological observations have further suggested that vestibular information underpins a strong link between the sense of self and awareness of one's own body. Individuals with peripheral vestibular disorders frequently report misperception of the shape, size, and location of their body parts (Sang et al., 2006; Lopez et al., 2008). Altered bodily representations have been described following artificial vestibular stimulation in neurological patients. For instance, artificial vestibular stimulation induces transient remission of disownership for body parts (*somatoparaphrenia*, Bisiach et al., 1991), somatoagnosia (Rode et al., 2012) and anosognosia (Cappa et al., 1987) caused by brain damage. Additionally, artificial vestibular stimulation modifies phantom limb sensations in both paraplegic (Le Chapelain et al., 2001) and amputee patients (André et al., 2001). More dramatically, vestibular dysfunction may contribute to autoscopic phenomena such as the impression of seeing one's own body in extrapersonal space (Blanke et al., 2005).

Here we review both neuropsychological observations and experimental results in healthy volunteers to argue that vestibular signals are fundamental for achieving a coherent representation of the body. Following Longo et al. (2010), we distinguished between three hierarchically-arranged levels of body representation, and we looked at whether vestibular signals might contribute to each of them (Figure 1). These are (i) somatosensation: "primary

sensory processing of somatic stimuli", (ii) somatoperception: "*the processes of constructing percepts and experiences of somatic objects and events, and of one's own body*" and (iii) somatorepresentation: knowledge about "*the body's character as a physical object in the external world*" (Longo et al., 2010). Thus, somatosensation refers to the primary processing of bodily sensations, while somatoperception involves an online percept of the state of the body, or of an object interacting with the body, based on the integration of multisensory inputs. Somatorepresentation refers to both explicit and implicit knowledge about the body, which may be less directly related to immediate input. The organisation of the components of this model is hierarchical: somatosensation is a necessary condition for somatoperception, because perceiving the current state of the body always involves integrating a range of somatosensory afferent signals. In contrast, somatorepresentation can persist in the absence of any particular somatosensory input: one knows what one's body is like even in the absence of any strong sensory input, for example after prolonged immobility, or while floating in water.

Longo at al.'s (2010) model highlights a duality in two classes of higher-order representations about the body. On the one hand, somatoperception refers to the *perceptual* process of constructing perceptual representations of the body. On the other, somatorepresentation refers to the *cognitive* process of constructing abstract knowledge about the body as a physical object (Longo et al., 2010). These processes differ in timescale as well as in their functions: somatoperception is online and short-lasting, while representations of the body may be retained over the long-term, potentially up to lifespan durations: many autobiographies demonstrate compelling long-term retention of first-person accounts of body knowledge. Merleau-Ponty, for example, alludes to this enduring quality of body knowledge: "We have found underneath the objective and detached knowledge of the body that other knowledge which we have of it in virtue of its always being with us and of the fact that we are our body" (Merleau-Ponty, 1962, p. 206).

However, interactions between body representations might occur. Longo et al. (2010) suggested that these interactions were primarily horizontal, between distinct types of

information at each level. For instance, tactile localization and body posture represent distinct and dissociable somatoperceptual representations (see below), yet there is evidence supporting functional interactions between them (Ho and Spence, 2007; Medina and Rapp, 2008). Vertical interactions between somatoperception and somatorepresentation are less likely to occur: for example, the ability to recognise one's own arm as belonging to one's own body (somatorepresentation) should be independent of the current posture of the arm (somatoperception). However, as neuropsychological evidence highlights, some between-level interactions exist. Nevertheless, it is plausible to hypothesise that vertical interactions and horizontal interactions require different computational principles. For instance, horizontal within-level interactions might be based on multisensory processes. Conversely, between-level vertical interactions might reflect cognitive hierarchical processes. Critically, Longo et al.'s (2010) model allows us to consider how vestibular signals *independently* contribute to low-level signal processing and to higher-order representations of the body. We suggest that each level of this somatic hierarchy can be influenced by vestibular signals (Figure 1).

**Vestibular contributions to somatosensation**

Somatosensation refers to the primary sensory processing of somatic stimuli, which principally occurs in the primary somatosensory cortices (Kaas, 1983; Mountcastle, 2005; Iwamura, 1998; Johnson and Hsiao, 1992; Romo and Salinas, 2001). For instance, it involves the ability to consciously detect and recognise somatosensory stimuli on the skin surface.

The influence of the vestibular system on somatosensation was first described by Vallar and colleagues in 1990 (Vallar et al., 1990), who investigated the effects of caloric vestibular stimulation on visuo-spatial hemineglect and associated somatosensory deficits. Caloric vestibular stimulation (CVS) is a routine diagnostic technique in the assessment of vestibular peripheral functionality (see Grabherr et al., 2015 for a review). This stimulation requires the irrigation of cold or warm water into the external ear canal (hereafter we refer to it as cold water irrigation, unless otherwise indicated). CVS elicits a movement of the semicircular canal fluid,

stimulating the afferent vestibular nerve which transmits the signals to the vestibular nuclei and activates the contralateral cortical and subcortical structures. Vallar et al. (1990) reported a transient amelioration of somatosensory deficits (*hemianaesthesia*) and many manifestations of the syndrome of visuo-spatial hemineglect in three right brain-damaged patients immediately after CVS (Vallar et al., 1990). This observation was replicated in a group study including both right brain-damaged and left brain-damaged patients (Vallar et al., 1993). Critically, the mirror-reversed paradigm, i.e. right ear CVS in right hemianaesthesia was unsuccessful: recovery of left hemianaesthesia was observed only in right brain-damaged patients following left ear CVS. The stimulation was generally ineffective in left brain-damaged patients, though it was effective in left brain-damaged patients presenting with visuo-spatial hemineglect (Vallar et al., 1993). This evidence suggested that CVS was only effective in restoring tactile perception because tactile deficits were associated with visuo-spatial neglect. Hemianaesthesia was therefore a manifestation of inattention for the neglected side of space (Vallar et al., 1990; Vallar et al., 1993). The temporary remission caused by CVS might have been induced by the indirect activation of an attentional orientation mechanism: CVS caused a shift of attention toward the neglected side of the body, re-activating normal somatosensation (Vallar et al., 1990; Vallar et al., 1993).

Similar remissions of somatosensory deficits have been observed by applying a different technique, namely galvanic vestibular stimulation. Galvanic vestibular stimulation (GVS) is a non-invasive technique which involves passing a weak direct current between surface electrodes placed behind the ear (see Fitzpatrick and Day, 2004 for a review). It is thought to stimulate the entire vestibular nerve, including both otolith and semicircular canal afferents (Stephan et al., 2005). In the traditional bilateral bipolar GVS configuration, an anode and cathode are placed on the left and right mastoid, or vice versa. Perilymphatic cathodal currents are thought to depolarize the trigger site and lead to excitation, whereas anodal currents hyperpolarize it resulting in inhibition (Goldberg et al., 1984). GVS evokes a sensation of head motion in space and disturbances of equilibrium (Fitzpatrick and Day, 2004). Crucially, the

polarity of stimulation can be reversed as part of the experimental procedure, producing opposite effects on firing rate in the two vestibular organs, and thus reversing of direction of the apparent head motion. GVS has been found to influence the inability to process or attend to the contralesional stimulus when two stimuli are simultaneously presented, in right brain-damaged patients (i.e. tactile extinction) (Kerkhoff et al., 2011; Schmidt et al., 2013a). This remission of tactile extinction is polarity-specific: left anodal and right cathodal GVS reduces tactile extinction in right brain-damaged patients. Importantly, a repeated number of GVS sessions can induce significant changes in tactile extinction that remains stable for several weeks (Kerkhoff et al., 2011; Schmidt et al., 2013a).

Although these clinical observations favour the idea that vestibular-induced remission of primary somatosensory deficits may be an attentional phenomenon (Utz et al., 2010; Utz et al., 2011; Miller et al., 2008), some evidence suggests that the influence of vestibular signals on somatosensation may be direct. First, the vestibular-induced remission of somatosensory deficits is dissociated from visuo-spatial hemineglect (Vallar et al., 1993). Although the majority of right brain-damaged patients with somatosensory deficits who were sensitive to vestibular stimulation also showed visuo-spatial hemineglect, Vallar et al. (1993) additionally described vestibular-induced remission of hemianaesthesia in two patients without visuo-spatial hemineglect. These observations suggest that vestibular stimulation might directly affect somatosensory processing, independently from its modulation of visuo-spatial attention. Importantly, it is known that primary somatosensory deficits and visuo-spatial neglect are double-dissociated disorders (Bisiach and Vallar, 1988). Second, it has been demonstrated that controlesional hemianaesthesia was ameliorated with comparable effects in both right brain-damaged and left brain-damaged patients who were administered with left ear CVS in order to selectively activate the right hemisphere vestibular projections (Bottini et al., 2005; see Bottini and Gandola 2015 for a review). Third, remission of somatosensory deficits has been described even in a patient affected by a lesion directly involving the primary somatosensory cortex (Bottini et al., 1995). Finally, the neural correlates of the vestibular-induced remission of left

hemianesthesia included activations in the right hemisphere involving the somatosensory cortices, insula, right putamen, inferior frontal gyrus in the premotor cortex (Bottini et al., 1995). Thus an undamaged subset of "sensory body representations" (cf. Bottini et al., 1995) may be able to mediate somatosensation when an appropriate physiological manipulation is introduced.

We recently hypothesised that vestibular signals might directly modulate the gain of the somatosensory afferent pathway, influencing somatosensation independently of spatial attention (Ferrè et al., 2011b; Ferrè et al., 2012; Ferrè et al., 2013b). Since this hypothesis proposes modality-specific changes in somatosensory processing, it is possible to distinguish it from non-specific attentional or spatial effects (Ferrè et al., 2011a; Ferrè et al., 2011b; Ferrè et al., 2013a). To test this hypothesis, CVS was administered in healthy participants (Ferrè et al., 2011b). The sensitivity to detect faint tactile stimuli applied on the index finger of both hands was estimated using signal detection. An enhancement of perceptual sensitivity was induced by left ear CVS. This effect was found for detection of somatosensory stimuli on both hands, i.e., ipsilateral and contralateral to the side of the vestibular stimulation. A visual detection task was administered in the same group of participants during the same testing session to control for arousal or attentional effects: no vestibular-induced modulation of visual sensitivity was found.

A similar experimental design combined with GVS confirmed such vestibular-induced enhancement. Left anodal and right cathodal GVS improved the ability to detect faint tactile stimuli (Ferrè et al., 2013a). The vestibular-induced enhancement was found for stimuli on both left and right hands, i.e. ipsilateral and contralateral to left anodal and right cathodal GVS. Right anodal and left cathodal GVS had no significant effects on somatosensory detection. Such polarity-specific influence on touch could reflect altered somatosensory processing in the right hemisphere. GVS produces polarity-dependent differences in a percept described as a *virtual rotation vector* (Day and Fitzpatrick, 2005) as well as sensory and cognitive functions in both healthy volunteers and brain-damaged patients (Utz et al., 2010). Neuroimaging studies have revealed asymmetrical cortical vestibular projections, suggesting that the core region of the

vestibular network is primarily located in the non-dominant right hemisphere in right-handed subjects (Bense et al., 2001; Suzuki et al., 2001; Dieterich et al., 2003; Janzen et al., 2008). Fink et al. (2003) used fMRI to study the effects of GVS. They found that left anodal and right cathodal GVS caused unilateral activation of the right hemisphere vestibular projections only. In contrast, the reversed polarity, right anodal and left cathodal stimulation, activated both left and right hemispheres. Thus, the right hemisphere vestibular projections are activated by both left anodal and right cathodal GVS and right anodal and left cathodal GVS (Eickhoff et al., 2006; Lopez et al., 2012a; Zu Eulenburg et al., 2011), yet the enhancement in somatosensory sensitivity was found only for left anodal and right cathodal GVS. Two alternative mechanisms could explain this vestibular modulation of somatosensation. First, GVS might diffusely activate an entire cerebral hemisphere by vestibular input, producing non-specific increases in cortical excitability (Utz et al., 2010). If the two hemispheres further differ in their contributions to somatosensation, then this might account for the described effects. Alternatively, vestibular input might specifically project to cortical areas within each hemisphere that are involved in somatosensation, such as the primary and secondary somatosensory cortices. However, fMRI studies identify a relatively stronger activation of the right hemisphere during left anodal and right cathodal GVS compared to the inverse polarity (Fink et al., 2003). Thus, it is not possible to exclude the possibility that the right-hemispheric activation during right anodal and left cathodal GVS was too weak to modulate the somatosensory processing.

Electrophysiological results also support the hypothesis of vestibular contributions to somatosensation. Somatosensory evoked potentials (SEPs) elicited by left median nerve showed a vestibular-induced modulation in the N80 component over both ipsilateral and contralateral somatosensory areas (Ferrè et al., 2012). The N80 component has been localised in the parietal operculum (area OP 1; Jung et al., 2009; Eickhoff et al., 2010), which functionally corresponds to the secondary somatosensory cortex (Eickhoff et al., 2010). The cortical area from which N80 is assumed to arise is immediately adjacent to the

neuroanatomical site of vestibular-somatosensory convergence in the human homologue of the monkey PIVC, identified as OP 2 (zu Eulenberg et al., 2012).

The multiply-connected nature of vestibular cortical anatomy suggests that vestibular signals might also participate in a multi-way interaction with several somatic signals (Ferrè et al., 2015a). For example, visual and vestibular signals might independently modulate somatosensation. Alternatively, vestibular signals might interact with the effects of vision on somatosensation, by facilitating or suppressing a visual signal that in turn influences somatosensation. A marker of the former arrangement would be that the effects of combined visual and vestibular stimulation should be predictable from independent effects of visual and of vestibular stimulation on somatosensation. Conversely, a marker of the latter arrangement would be that results of trimodal stimulation differ from simple superposition of vestibular-somatosensory and visual-somatosensory response patterns. This hypothesis has been recently investigated (Ferrè et al., 2015a). Participants were instructed to detect faint somatosensory stimuli delivered to the left index finger. A visual signal occurred close to the finger in some trials. A near infra-red caloric vestibular stimulus was used to artificially activate the vestibular organs. Near infra-red CVS is a recently-developed technique that artificially stimulates the vestibular system by a gradual non-contact thermal stimulation of the horizontal semicircular canals via the external auditory canal (Ferrè et al., 2015a). Both visual and vestibular events increased somatosensory sensitivity. Critically, no evidence for supra-additive multisensory enhancement emerged when both visual and vestibular signals were administered together. Visual and vestibular inputs have therefore facilitatory influences on somatosensory processing, while vestibular inputs additionally suppress visual processing, consistently with known neuroanatomical interactions between vestibular, visual and somatosensory systems (Ferrè et al., 2015a).

Vestibular stimulation has dramatically different effects *within* the somatosensory system. A reduction of chronic pain has been demonstrated in patients affected by right brain-damage (McGeoch et al., 2008a; Ramachandran et al., 2007; McGeoch et al., 2008b). At least

two alternative mechanisms have been suggested to explain these effects (McGeoch et al., 2008a; Ramachandran et al., 2007; McGeoch et al., 2008b). First, pain relief may be caused by activation of the thermosensory cortex in the dorsal posterior insula adjacent to PIVC stimulated by the vestibular stimulation. Alternatively, the PIVC itself may be part of the interoceptive system and have a direct role in pain control. In a recent study, psychophysical thresholds for touch and pain were estimated in healthy participants immediately before and after CVS (Ferrè et al., 2013b). Results confirmed a vestibular-induced enhancement of touch, but revealed a reduction in levels of pain (Aδ nociceptors) (Ferrè et al., 2013b). To clarify the neural mechanisms underlying such vestibular-induced *analgesia*, CVS has been combined with electrocortical responses elicited by nociceptive-specific laser stimulation (laser-evoked potentials, LEPs) (Ferrè et al., 2015b). CVS resulted in a significant reduction of the amplitude of all LEP components, including the early N1 wave which reflects the first arrival of nociceptive input to primary somatosensory cortex. The analgesic effect induced by CVS could be mediated by either subcortical gating of the ascending nociceptive input, or by direct modulation of the primary somatosensory cortex. A striking feature of the vestibular contribution to somatosensation, therefore, is the independent modulation of distinct somatosensory submodalities. Enhancement in tactile system demonstrates an up-regulation of tactile processing, while reduction of the level of pain demonstrates a down-regulation of nociceptive processing. The vestibular system modulates connections with different somatosensory submodalities, regulating the activity in multiple sensory systems independently.

**Vestibular contributions to somatoperception**

*Somatoperception* refers to the processes of constructing percepts and experiences of somatic objects and events, and of one's own body (Longo et al., 2010). The body is the vehicle for perception: percepts of stimuli applied on the skin surface must be referenced to pre-existing representations of the body. However, the body can also be a direct object of perception. This is seen in the process of constructing explicit models of body form (*body image*, a percept of

what my body is), and the configuration of body parts (*postural schema*, a percept of where my body is). Vestibular signals contribute to cases in which the body is a vehicle for perception, and to cases in which it is itself the object of perception.

*Localisation of touch on body surface*

The ability to localise touches on the skin surface (*topognosis*) is essential to successfully interact with the surrounding environment. Localising the stimulus within a somatotopic map is not by itself sufficient to identify its position on the body surface. Rather, a two-stage process is required (Longo et al., 2010). First, the stimulus is localised within the somatotopic map. Second, the somatotopic location must be mapped onto a corresponding bodily location. This second step requires a body model, relating the receptor surface of the skin to locations on the body, and thus involving an implicit somatoperception. Consistent with this model for somatoperception, localising a tactile stimulus requires both the somatotopic maps in the primary somatosensory cortex (Seyal et al., 1997), and also additional somatosensory processes in parietal areas posterior to the primary somatosensory cortex (Porro et al., 2007; Van Boven et al., 2005).

A recent study investigated the effect of GVS on the localisation of stimuli on the skin of the hand (Ferrè et al., 2013c). Vestibular inputs interfered with the localisation of touches on the dorsum of the hand. This bias was selective for the proximal-distal axis: stimuli on the hand were shifted toward the wrist. Importantly, this shift has been showed to follow a clear spatial gradient, with a bias in the proximal direction for touches located on the dorsum, and toward the distal direction for touches located on the fingers. Specific polarities of GVS had differential effects on localisation of touch. In particular, the proximal shift in tactile localisation was stronger during right anodal and left cathodal GVS than left anodal and right cathodal GVS. Such hemisphere-specific effects might be due to the potential hemispheric lateralisation of the ability to localise touch. Indeed, the observed vestibular-induced effects on tactile localisation are reminiscent of those described in patients following left brain-damage. Clinical

observations described patients affected by left parietal lesions showing errors of tactile localisation in the contralesional hand (Rapp et al., 2002). These localisation errors preserved the somatotopic arrangement of the hand, but systematically misplaced each point toward the proximal direction (Rapp et al., 2002). Rapp et al. (2002) reported two patients showing a clear dissociation between an intact ability to detect faint tactile stimuli compared to an impaired localisation of touches on the affected hand. In particular, the authors commented "the post-lesion [tactile] mislocalisations may preserve the relative locations of the pre-lesion topography, resulting in systematically shifted and distorted somatosensory experiences".

Neuroimaging studies reveal activation of the right temporo-parietal junction during tactile localisation (Van Boven et al., 2005). This area is also a core region of the human vestibular cortical network (Lobel et al., 1999; Fasold et al., 2002). The anatomical overlap between vestibular cortical areas and areas involved in tactile localisation suggests that vestibular inputs might influence the process of registering somatotopic skin location with specific locations on the body, although this should be tested in further studies, possibly investigating tactile localisations in patients with peripheral vestibular disease.

*Proprioceptive localisation of body parts in external space*

Proprioceptive information from mechanoreceptors in joints, muscles, tendons, and stretch-sensitive receptors in the skin describe the configuration of the body in terms of the degree of flexion or extension of each joint (Burgess et al., 1982). The localisation of body parts in space requires a combination of afferent information and stored representations of the body. Head and Holmes (1911) introduced the notion of the *postural schema* to refer to the continuously updated representation of the posture of the body.

Artificial vestibular stimulation has been showed to ameliorate proprioceptive deficits in right brain-damaged patients. Specifically, left anodal and right cathodal GVS improved the accuracy in detecting the position of the left arm in seven visuo-spatial hemineglect patients: these effects were observed during online stimulation and also after 20 minutes from the

stimulation (Schmidt et al., 2013b). Vestibular signals might have provided additional sensory input to help in localising the correct position of the arm. It has been suggested that such facilitatory vestibular effects may rely on the activation of intact structures that are involved in the recalibration of body and limb position in space. Importantly, neither right anodal and left cathodal GVS nor sham stimulation influenced the proprioceptive localisation of the arm, ruling out attentional or unspecific effects. The differential effects of left anodal and right cathodal GVS compared with right anodal and left cathodal GVS might be, once again, related with the asymmetry of the cortical vestibular network (Dieterich et al., 2003).

Vestibular effects on the localisation of body parts in space have been observed in healthy participants (Schmidt et al., 2013c). Left anodal and right cathodal GVS caused a transient disruption of left arm localisation in right-handed participants. These results have been interpreted as a vestibular-induced interference with arm positioning which is particular salient in right-handers due to the anatomical asymmetry of the vestibular system (Schmidt et al., 2013c; Dieterich et al., 2003). Similarly, it has been reported that GVS disrupted reaching movements towards a visual target by interfering with the spatial estimate of where the hands are in the surrounding space (Bresciani et al., 2002).

**Vestibular contributions to somatorepresentation**

*Somatorepresentation* involves the on-line construction of higher-level percepts related to the body. This representation is not merely an abstract conceptualisation, but actually underlies all bodily experience, for the reasons that we describe below.

*Model of body shape and size*

No peripheral receptors are directly informative about shape and size of body parts, and therefore the knowledge about these features are linked to an internal stored model of the body's metric properties (Longo and Haggard, 2010). It has been demonstrated that this *body model* is strongly distorted (Longo and Haggard, 2010). At least for the hand, these distortions included

a radial–ulnar gradient of magnification of the digits and shrinkage toward the proximo–distal axis. These internal models appear to be independent of any specific somatosensory input for two reasons. First, people can judge the configuration and location of the body, including its metric properties, in the absence of specific somatosensory stimulation (Longo and Haggard, 2010). Second, these metric properties are accessible even for congenital phantoms (Longo et al., 2012). For this reason, the internal body model involves a level of *somatorepresentation*, independent of any particular somatosensory event or stimulus.

A contribution of vestibular signals to the metric body model is evident from clinical observations in patients affected by peripheral vestibular disorders. Bonnier (1905) described distortions of the representation of body shape and size, such as "[the patient] felt his head become enormous, immense, losing itself in the air" and "her vertigo gave her the sensation that she no longer exists as a body" (Bonnier, 1905).

The relation between vestibular signals and the metric body model has been investigated using CVS in psychophysical paradigm in healthy participants. Lopez et al. (2012b) asked participants to point to different anatomical landmarks on the left hand (knuckles and tip of the fingers) without seeing them, immediately before and after CVS. The perceived length and width of the hand were estimated based on these judgments. CVS significantly increased both the perceived length and width of the hand. These data are comparable with clinical observations of vestibular peripheral patients ("extremities had become larger", Schilder, 1935; see Lopez 2015 for a review). However, no such effects were found in a similar task combined with low-intensity GVS (Ferrè et al., 2013c). This may be due to differences in the vestibular stimulation technique used. For instance, GVS effects are relatively weak compared to the CVS. Further studies need to clarify those differences.

*Ownership of body parts*

The sense of body ownership is often described as a feeling of *mineness*, that one's body belongs to oneself (Metzinger, 2003). The most convincing evidence for such a concept comes

from disordered body representation in neuropsychological patients. For example, right brain-damaged patients with *somatoparaphrenia* lack the normal sense of the body as a coherent entity, as to the feeling that one's body belongs to oneself (Gallagher, 2000). For example, they may have delusional beliefs that their own limbs belong to someone else (Vallar and Ronchi, 2009). Traditionally, a strong emphasis has been put on the role of visual and somatosensory signals in body ownership. This is because ownership of body parts strongly relies on the visual feedback from one's own actions and the somatosensory feedback from this action (Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005). However, other sensory modalities potentially contribute to body ownership.

Studies of individual cases described temporary remissions of somatoparaphrenia following artificial vestibular stimulation (Bisiach et al., 1991; Rode et al., 1992; Schiff and Pulver, 1999). As described in Bisiach et al. (1991), "A.R. would unhesitatingly attribute her left upper limb to her mother, [but] under the effect of vestibular stimulation she unhesitatingly recognizes that same arm as her own". Recently, CVS was reported to reduce somatoparaphrenia for the right hand also in a left brain-damaged patient (Ronchi et al., 2013). Injection of cold water in the right auditory canal transitory ameliorated the delusional belief that the patient's right hand did not belong to her.

The hypothesis that vestibular inputs contribute to the sense of ownership has been explored in healthy participants using the Rubber Hand Illusion paradigm (RHI, Botvinick and Cohen, 1998). A rubber hand viewed in peripersonal space is experienced as part of one's body if it is touched in synchrony with the participant's own unseen hand. RHI involves a transposition of the sense of body from one object to another, rather than addition of a new body part (Longo et al., 2008; Moseley et al., 2008; Barnsley et al., 2011). That is, dis-ownership of one's own hand accompanies the increased sense of ownership over the rubber hand. Consistent with this account, participants then mislocate their own hand as closer to the fake hand than it actually is. This *proprioceptive drift* increases with the increasing strength of the illusion (Botvinick and Cohen, 1998), and provides a quantitative proxy for assessing bodily

awareness (Longo et al., 2008). Combining RHI with GVS revealed once again a polarity dependent vestibular modulation of the strength of the RHI illusion (Ferrè et al., 2015c). Left anodal and right cathodal GVS, which predominantly activates the vestibular projections in the right hemisphere, produced a smaller proprioceptive shift toward the rubber hand compared with the opposite polarity (Ferrè et al., 2015c). The right hemisphere vestibular network therefore increases the salience of intrinsic somatosensory and proprioceptive signals about hand position, and decreases the salience of visual information responsible for visual capture during the RHI. However, Lopez et al. (2010) found a vestibular induced enhancement of the RHI as measured by questionnaires, but no reliable effects on proprioceptive drift. While it is difficult to reconcile results from these studies, it is notable that proprioceptive drift (Ferrè et al., 2015) and questionnaires (Lopez et al., 2010) are two different and independent aspects of the RHI (Rohde et al., 2011).

Vestibular contributions to other disorders involving abnormal forms of body ownership have been proposed. Ramachandran and McGeoch (2007) hypothesised that vestibular stimulation could be used to treat patients with a desire for amputation of healthy body parts, a disorder known as Body Identity Integrity Disorder (BIID). On one hypothesis, BIID reflects a mismatch between a neural representation of the actual anatomical body, and a second (unidentified) representation of the desired body form (Ramachandran and McGeoch, 2007). Blanke et al. (2009) suggested that BIID can be considered a chronic form of asomatognosia, essentially a negative phantom limb. A recent study tested Ramachandran's hypothesis in a group of 13 BIID patients (Lenggenhager et al., 2014). Neither left nor right ear CVS reduced their desire for amputation. The underlying mechanisms of BIID may be just different compared somatoparaphrenia: while BIID is a long-term condition that has often been consolidated since childhood (Brugger et al., 2013), somatoparaphrenia can be observed during the acute phase after brain injury and may be more prone to modulations by artificial vestibular stimulation.

*First-person perspective*

An important aspect of the representation of our body is the consistent first-person perspective on the external world. Indeed, almost all our bodily experiences are tagged by a first-person perspective. Vestibular damage can often produce psychiatric symptoms of depersonalisation, defined as the subjective experience of unreality and detachment from the self", and derealisation, the experience of the external world appearing strange or unreal (Sang et al., 2006; Jauregui-Renaud et al., 2008; see Jauregui-Renaud, 2015 for a review). Similar feelings of unreality have also been found in healthy participants undergoing artificial vestibular stimulation (Sang et al., 2006).

*Out-of-body experiences*, in which neurological patients localise the self outside their own body and experience seeing their body from this disembodied location, represents a failure in the first person perspective and were attributed to conflicting visual, somatosensory and vestibular information (Brugger et al., 1997). Interestingly, out-of-body experiences are frequently associated with vestibular sensations, such as the feeling of floating in the room, levitation and lightness (Blanke and Mohr, 2005; Blanke et al., 2004; Heydrich and Blanke, 2011). The vestibular contribution to these phenomena is further supported by the association between out-of-body experience and temporo-parietal junction and insula (Blanke et al. 2004), which are considered the two main regions receiving vestibular projections (Heydrich and Blanke, 2013; Ionta et al., 2011, Mazzola et al., 2014; Pfeiffer et al., 2014).

One can therefore hypothesize that a fundamental function of the vestibular input might be to provide the normal first-person perspective on the world. Ferrè et al. (2014) investigated whether vestibular signals influence the perspective people take (first-person perspective vs third-person perspective) in interpreting ambiguous stimuli applied on the skin surface (e.g. graphesthesia task, Natsoulas and Dubanoski, 1964). For example, when an experimenter draws the letter *b* on the forehead of a blindfolded participant, the participant may perceive the stimulus either from an external third-person perspective (reading it as "b"), or from an internal first-person perspective (reading it as "d"). Prevalence of one judgement over the other

provides an implicit measure of whether the perceiver's perspective on the stimulus originates from within his body, or from outside it. Low intensity GVS inputs promote first-person perspective judgements, augmenting a natural vestibular contribution to embodiment. Disembodied experiences, as out-of-body phenomena, may require different stimulation patterns, stronger intensities, direct stimulation of vestibular cortical areas rather than the vestibular periphery, or combined with additional visual and somatosensory mismatches (Blanke et al., 2002; Blanke et al., 2012).

Critically, disruptive vestibular signals have been showed to interfere with the so-called *self-advantage* effect: when people are asked to detect asynchrony between self-generated movement and the visual feedback concerning that movement, they are more sensitive when the feedback is presented from a first-person perspective (Hoover and Harris, 2012; Hoover and Harris, 2015). Hoover and Harris (2015) recently investigated whether artificially disruptive vestibular stimulation affects the self-advantage effect. Participants performed movements while viewing their hand in a first-person or third-person perspective. They judged which of two experiences involved a delayed visual feedback, while disruptive GVS was applied. Disruptive GVS abolished the self-advantage, so there was no longer any difference in performance between first-person and third-person perspectives. These data further support the idea that functional vestibular information is essential in distinguishing between self and other, and in maintaining a coherent sense of ownership over body parts.

## Outlook

Textbooks still consider the vestibular system as an organ for balance and orienting eye movements. However, signals from the vestibular system make a crucial contribution to most everyday adaptive behaviours. Accordingly, vestibular information interacts widely with sensory and cognitive processes (Balaban et al., 2011).

Clinical observations and experimental evidence reviewed here suggests a key contribution of vestibular signals to bodily representations. The present review article aimed at

organising the existing knowledge to identify *whether* and *how* vestibular signals influence body representations. As summarised above, the vestibular system strongly contributes to the somatosensational, somatoperceptional and somatorepresentational components of bodily awareness (Figure 1). Specifically, vestibular signals *independently* contribute to low-level signal processing and also to higher-order representations of the body. Vestibular information directly modulates the primary processing of somatic sensations, but also the on-line percept of the state of the body. There is evidence that it influences processing within other individual sensory channels, rather than simply adding an extra ingredient to the multisensory mix. Our review also highlights an independent vestibular modulation in two classes of higher-order representations about the body. On the one hand, vestibular information influences somatoperception (the *perceptual* process of constructing perceptual representations of the body). On the other, vestibular information contributes to somatorepresentation (the *cognitive* process of constructing abstract knowledge about the body) (Longo et al., 2010). Importantly, several lines of evidence rule out explanations based on changes in arousal, and spatial attention. Rather, each level of the somatic hierarchy can be influenced by vestibular signals. However, more work is needed to improve our understanding of the neurophysiological mechanisms supporting the described vestibular effects.

Balaban and colleagues (2011) have recently proposed a model in which vestibular signals are tightly interwoven with three different biochemical pathways to serve sensorimotor processing, cognition and interoception. Critically, this arrangement implies that alterations within one pathway may elicit functional changes in the others (cf. the well-known comorbidity of balance, anxiety and migraine; Yardley, 2000). Vestibular-induced changes in body representations, be these through experimental or clinical phenomena, may therefore modulate processing within allied cognitive and interoceptive domains. Some evidence already supports this neural influence, for example deficits in somatosensation are often present in association with cognitive, attentional, impairments. Here, we have proposed a multicomponent account for bodily awareness and identified multiple independent vestibular contributions to it. We

hope that this account will open new avenues of research in the field and propose that future neuroscientific investigations should focus on how vestibular-induced changes in body representations may interact with other neural systems.

Under normal circumstances, every movement of the head implies a new relation between the body-self and the external world. We suggest that vestibular contributions to body representations may arise from a neural circuit that optimizes the balance between gathering information from personal/peripersonal space immediately surrounding the body, and farther environmental space. Evidence showed strong vestibular modulation of somatic sensation, perception and representation. Interestingly, these effects could be interpreted as enhancement of the bodily self: vestibular signals rebalance sensory events away from the world and towards the self.

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**Figure caption**

**Figure 1. Vestibular contributions to bodily representations.**

A schematic of the vestibular contributions to bodily representations. According with Longo at al.'s (2010) model, we distinguish between three hierarchical levels of body representation. These are (i) *somatosensation*, the primary sensory processing of somatic stimuli, (ii) *somatoperception*, the processes of constructing percepts and experiences of somatic objects and events and (iii) *somatorepresentation*, the knowledge about the body as a physical object in the world. Vestibular signals independently contribute to low-level signal processing and also to higher-order representations of the body.

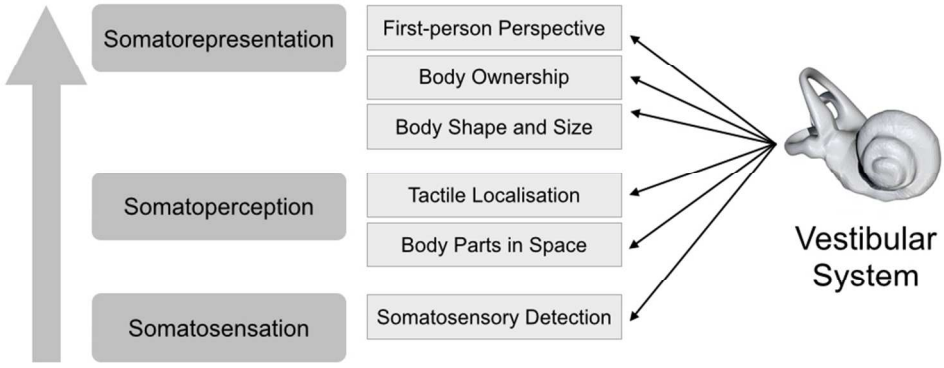


Figure 1. Vestibular contributions to bodily representations.\r\nA schematic of the vestibular contributions to bodily representations. According with Longo at al.'s (2010) model, we distinguish between three hierarchical levels of body representation. These are (i) somatosensation, the primary sensory processing of somatic stimuli, (ii) somatoperception, the processes of constructing percepts and experiences of somatic objects and events and (iii) somatorepresentation, the knowledge about the body as a physical object in the world. Vestibular signals independently contribute to low-level signal processing and also to higher-order representations of the body.